

Host Plant Reactions, Some Properties, and Serology of Wild Potato Mosaic Virus

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ABSTRACT

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A virus for which the name wild potato mosaic virus (WPMV) is proposed was isolated from plants of the wild potato species *Solanum chancayense* growing in the lomas vegetation in the Peruvian coastal desert; infected plants showed symptoms of severe mosaic and leaf deformation. The host range of WPMV was restricted to certain species in five solanaceous genera. *Nicotiana bigelovii*, *N. clevelandii*, and *N. occidentalis* were useful indicator hosts, and *N. rustica* reacted with local lesions. The virus infected systemically seven of 16 wild, tuber-forming, *Solanum* spp. including *S. chancayense* and *S. mochicense*. However, none of the 13 potato cultivars tested became infected. The virus was readily transmitted after acquisition periods of 30 sec or 1 min by the aphid *Myzus persicae*.

Additional key words: potato virus, serology.

Nicotiana clevelandii leaf sap remained infective when diluted to 10^{-3} but not to 10^{-4} , when heated at 60 C but not at 65 C, and when stored for 5 but not 6 days. Electron microscopy of infective sap revealed long flexuous particles about 735 nm in length, typical of the potato virus Y (potyvirus) group. In microprecipitin grid titration tests, antiserum to WPMV reacted with partially purified antigens of eight different potyviruses from solanaceous hosts, and antisera to three of these reacted with WPMV in reciprocal tests. The virus was most closely related serologically to Peru tomato virus, tobacco vein mottling virus and to potato virus Y. However, differences in its host range and symptomatology clearly distinguished WPMV from these three viruses.

RESUMEN

Un virus para el cual se propone el nombre de wild potato mosaic virus (WPMV) fue aislado de plantas enfermas de la papa silvestre *Solanum chancayense* que crece en las lomas del desierto de la costa Peruana. Los síntomas fueron mosaico severo y deformación de hojas. El rango de hospederos del WPMV está restringido a ciertas especies en solamente cinco géneros de solanáceas. *Nicotiana bigelovii*, *N. clevelandii*, y *N. occidentalis* fueron hospederos indicadores útiles y *N. rustica* reaccionó con lesiones locales. El virus infectó sistemáticamente siete de 16 especies de papas silvestres incluyendo *S. chancayense* y *S. mochicense*. Sin embargo, ninguno de 13 cultivares de papa fueron infectados. Fue transmitido con facilidad después de períodos de adquisición de 30 seg y 1 min por el áfido *Myzus persicae*. Jugo de *N. clevelandii* permaneció infectivo cuando se

Palabras claves adicionales: Virus de papa, serología.

diluyó a 10^{-3} pero no a 10^{-4} , cuando se calentó a 60 C pero no a 65 C, y cuando se almacenó por 5 pero no 6 días. Microscopía electrónica de jugo infectivo reveló la presencia de partículas alargadas flexuosas de aproximadamente 735 nm de longitud típicas del grupo del virus Y de la papa (potyvirus). En pruebas de microprecipitación en placas de petri, antisuero de WPMV reaccionó con antígenos parcialmente purificados de ocho potyvirus diferentes que atacan solanáceas y antisueros de 3 de ellos reaccionaron con WPMV en pruebas recíprocas. Serológicamente, el virus fue más cercanamente relacionado al Perú tomato virus, tobacco vein mottling virus y al virus Y de la papa. Sin embargo, las diferencias en el rango de hospederos y sintomatología permitió distinguir claramente WPMV de estos tres, reforzando su clasificación como un nuevo potyvirus.

In the winter of 1974, plants of *Solanum chancayense* Ochoa with severe mosaic and leaf deformation were found growing in the lomas vegetation in the Peruvian coastal desert at Lachay near Lima. The lomas are hilly areas where low clouds during the winter give sufficient moisture to support growth, temporarily, of short-lived plants adapted to this habitat, including several wild potato species (10). When an isolate obtained from diseased *S. chancayense* by inoculation to plants of *Nicotiana clevelandii* Gray was examined by electron microscopy, particles typical of the potato virus Y group, the potyviruses, were found (4,6). This paper describes the properties of this virus, which we call wild potato mosaic (WPMV), and shows it to be a distinct potyvirus.

MATERIALS AND METHODS

Virus cultures. WPMV was cultured in plants of *N. clevelandii*, *N. occidentalis* Wheeler, and *N. bigelovii* Wats. and these hosts were used as sources of inocula for the experiments. Either *N. occidentalis* or *N. debneyi* Domin. were used to culture the

following other potyviruses (names of donors in parentheses): Colombian datura virus (CDV), henbane mosaic virus (HMV), and potato virus A (PVA) (R. Koenig); tobacco vein mottling virus (TVMV) (G. V. Gooding); tobacco etch virus (TEV) (D. E. Purcifull); pepper vein mottle virus (PVMV) (R. H. Kenten); and Peru tomato virus (PTV) strain C plus potato virus Y (PVY) common strain isolated in Peru (5).

Plants. Indicator hosts came from seedlings transplanted to pots containing either sterilized muck soil or a mixture of sterilized soil, sand, and peat. Sources and propagation of wild tuberous *Solanum* species and potato cultivars were as described previously (5).

Tests were done under greenhouse conditions at 18–22 C. Mechanical inoculations were made by rubbing 22- μ m (600-mesh) Carborundum-dusted leaves with sap inoculum. Plants were tested for infection by back-inoculation to *N. bigelovii* or *N. clevelandii*. For study of properties in infective sap, inoculations were made to groups of three to six plants of either species.

Aphid transmission tests. These were done as previously described (5).

Electron microscopy. Samples were processed as previously described (5).

Purification and serology. The virus was purified by the procedures described previously (5).

An antiserum to WPMV was produced as described previously (5) except that intramuscular injections were made four times at weekly intervals. This antiserum was compared in microprecipitin tests with the eight potyviruses mentioned above and antisera (from the same donors) to all except CDV and HMV also were compared in reciprocal tests. Procedures for the preparation of antigens and serological tests were as in (5) and (1), respectively.

RESULTS

Disease symptoms. Disease symptoms in *S. chancayense* are leaf deformation, especially of young leaves, and a general severe mosaic (Fig. 1C). In the lomas vegetation at Lachay, plants of this species normally grow in small groups among rocks. Within a group, plants are usually either uniformly diseased or uniformly healthy in appearance. In 1976, 60% of the groups examined were diseased.

Host range and symptomatology. Wild potato mosaic virus infected 20 solanaceous species (Table 1). Mosaic or symptomless infection were the normal responses. The following 37 species in 10 different families developed no symptoms when inoculated with WPMV and no virus was detected in them by backtesting to indicator hosts: *Amaranthus caudatus* L., *A. edulis* L., *Gomphrena globosa* L. (Amaranthaceae); *Chenopodium amaranticolor* Coste & Reyn., *C. murale* L., *C. quinoa* Willd. (Chenopodiaceae); *Zinnia elegans* Jacq. (Compositae); *Brassica pekinensis* (Lour.) Rupr. (Cruciferae); *Cucumis sativus* L., *Cucurbita pepo* L. (Cucurbitaceae); *Ocimum basilicum* L. (Labiatae); *Clitorea ternatea* L., *Cyamopsis tetragonoloba* Taub., *Dolichos gibbosus* Thunb., *Phaseolus aborigineus* Burkart, *P. acutifolius* Gray 'Latifolius', *P. calcaratus* Roxb., *P. vulgaris* L. 'Monroe', 'Pinto', 'Prince', and 'Top Crop', *Vigna cylindrica* Skeels, *V. sinensis* (Torn.) Savi 'Black' (Leguminosae); *Sesamum indicum* L. (Pedaliaceae); *Capsicum sinensis* Murr. 'Colorado tambeno', 'Mono rojo', and 'Panca', *Datura stramonium* L., *Lycopersicon chilense* Dun., *L. peruvianum* (L.) Mill., *L. pimpinellifolium* (Jusl.) Mill., *Nicotiana glutinosa* L., *Physalis peruviana* L., *Solanum brevidens* Phil. (PI

245764), *S. cardiophyllum* Lindl. (PI 275215), *S. curtilobum* Juz. & Buk. (PI 186181), *S. demissum* Lindl. (PI 230579), *S. demissum* 'A', *S. demissum* 'Y', *S. demissum* × *S. tuberosum* L. 'A6', *S. stenotomum* Juz. & Buk. (PI 230512), *S. stoloniferum* Schlecht. (PI 230557), *S. tuberosum* subsp. *andigena* Juz. & Buk. 'Ccompis', 'Chata Blanca', 'Sipeña', 'Renacimiento', *S. tuberosum* subsp. *tuberosum* L. 'Arran Pilot', 'Pentland Crown', 'Pentland Dell', 'Pentland Ivory', 'Maris Peer', subsp. *tuberosum* × subsp. *andigena* 'Mariva', 'Merpata', 'Ranrahira', 'Revolución' (Solanaceae); and *Anthriscus cerefolium* Hoffm., *Coriandrum sativum* L. (Umbelliferae). The host range of WPMV thus seems narrow, restricted to certain Solanaceae.

The most widely used hosts were *N. clevelandii*, which developed a distinct mosaic (Fig. 1A), and *N. bigelovii*, which reacted with a distinct blotchy mosaic/mottle plus twisting and deformation of young leaves. *Nicotiana occidentalis* reacted initially with systemic vein clearing followed by a mild mosaic and some leaf curling. Distinctive symptoms also were produced in tobacco (*N. tabacum* 'Samsun') and *N. rustica*. In the former, lower noninoculated leaves reacted with initial chlorotic blotching followed by necrotic spotting and formation of broken necrotic rings and broken lines which ran alongside veins (Fig. 1B); upper noninoculated leaves became symptomlessly infected. In inoculated leaves of *N. rustica*, distinct chlorotic blotches developed, many of which later became surrounded by brown necrotic rings (Fig. 1D). Systemic infection usually was symptomless, but sometimes systemic chlorotic blotches formed.

Seven of the 16 wild tuber-bearing *Solanum* species inoculated with WPMV became infected systemically. *Solanum chancayense* (PI 338615) reacted with symptoms of deformation of young leaves and generalized severe mosaic similar to those found in naturally-infected plants. *Solanum mochicense* Ochoa (PI 283114) which is also from the lomas vegetation reacted similarly. *Solanum megistacrolobum* Bitt. (PI 275147) developed a mild mosaic. The other four *Solanum* spp. infected systemically developed no symptoms and in three further species infection was restricted to inoculated leaves. Repeated attempts to infect *S. demissum* 'A' and 'Y' and clone 'A6', which are diagnostic indicator hosts for PVA and PVY, failed, but *S. demissum* PI 175404 became infected without visible symptoms. Also, WPMV did not infect five British and eight Peruvian potato cultivars, and two species which are cultivated in some parts of the Andean highlands of Peru, *S. curtilobum* and *S. stenotomum*.

Symptomatology comparison with eight other potyviruses. Eight different potyviruses that infect solanaceous hosts were inoculated to *S. chancayense* and *S. mochicense* to see if they produced symptoms resembling those induced by WPMV in these species. These viruses also were inoculated to *N. rustica* (Table 2). All viruses produced mosaics in *S. chancayense*, which were severe

TABLE 1. Symptomatology of wild potato mosaic virus in indicator hosts and wild potatoes

Species	Symptoms ^a
<i>Lycopersicon esculentum</i> Mill. 'Kondine Red' and 'Rutgers'	SS
<i>Nicandra physaloides</i> Gaertn.	SM
<i>Nicotiana benthamiana</i> Domin.	SS
<i>N. bigelovii</i> Wats.	SM,Df
<i>N. clevelandii</i> Gray	SM
<i>N. debneyi</i> Domin.	SS
<i>N. occidentalis</i> Wheeler	VC,MM,Cu
<i>N. rustica</i> L.	LCB,LNR,SCB, SS
<i>N. tabacum</i> L. 'Samsun'	SNS,SNR,SCB
<i>Physalis floridana</i> Rydb.	MM
<i>Solanum berthaultii</i> Hawkes (PI 265857)	SI
<i>S. brachycarpum</i> Corr. (PI 275180)	SS
<i>S. chacoense</i> Bitt. (PI 275136)	SS
<i>S. chancayense</i> Ochoa (PI 338615)	SM,Df
<i>S. demissum</i> Lindl. (PI 175405)	SS
<i>S. megistacrolobum</i> Bitt. (PI 275147)	MM
<i>S. microdontum</i> Bitt. (PI OKA 4820)	SI
<i>S. mochicense</i> Ochoa (PI 283114)	SM,Df
<i>S. raphanifolium</i> Card & Hawkes (PI 210048)	SS
<i>S. vernei</i> Bitt. & Wittm. (PI 230468)	SI

^aCoded symptom descriptions: LCB = local chlorotic blotches; LNR = local brown necrotic rings; SI = symptomless infection in inoculated leaves only; Cu = leaf curling; Df = leaf deformation; MM = mild mosaic; SM = strong mosaic; SCB = systemic chlorotic blotches; SNR = systemic necrotic broken rings and line patterns; SNS = systemic necrotic spotting; VC = vein clearing; and SS = symptomless systemic infection.

TABLE 2. Reactions of *Nicotiana rustica*, *Solanum chancayense* (PI 338615) and *Solanum mochicense* (PI 283114) to eight potyviruses from the Solanaceae^a

Virus	Host reactions ^b of:		
	<i>N. rustica</i>	<i>S. chancayense</i>	<i>S. mochicense</i>
PTV	MM	SM,SNS	SCS
PVY	MM	LCS,SM,Df	SM
PVA	LNR,LCS,SS	LCS,VC,MM	SS
TVMV	MM	VC,MM	SS
TEV	VC,MM	LCS,SM	LCS,VC,MM,SCS
PVMV	LNR,SS	LNS,SM,SCS,Df	LCS,SCS
CDV	VC,SM,Df	LCS,SM	SM
HMV	SM,Df	LCS,SM	MM

^aBack inoculations to *N. debneyi* or *N. occidentalis* were made to confirm presence of the different viruses.

^bCoded symptom descriptions: LCS = local chlorotic spots or blotches; LNR = occasional local large white necrotic rings; LNS = local brown necrotic spots; Df = leaf deformation; MM = mild mosaic; SM = strong mosaic or chlorotic mottle; SCS = systemic chlorotic spotting or blotching; SNS = systemic necrotic spotting; VC = systemic vein clearing; SS = symptomless systemic infection.

except with PVA and TVMV. PVY induced systemic symptoms most closely resembling those of WPMV (severe mosaic and deformation of young leaves) but also produced many faint chlorotic spots in inoculated leaves. PVMV caused the most severe symptoms. In *S. mochicense* only CDV and PVY caused severe

mosaics and none of the viruses caused leaf deformation. In *N. rustica*, only PVA and PVMV caused symptoms in inoculated leaves but in neither instance did these resemble those induced by WPMV. Those of PVA were diffuse chlorotic blotches plus occasional white necrotic rings and PVMV caused just a few large

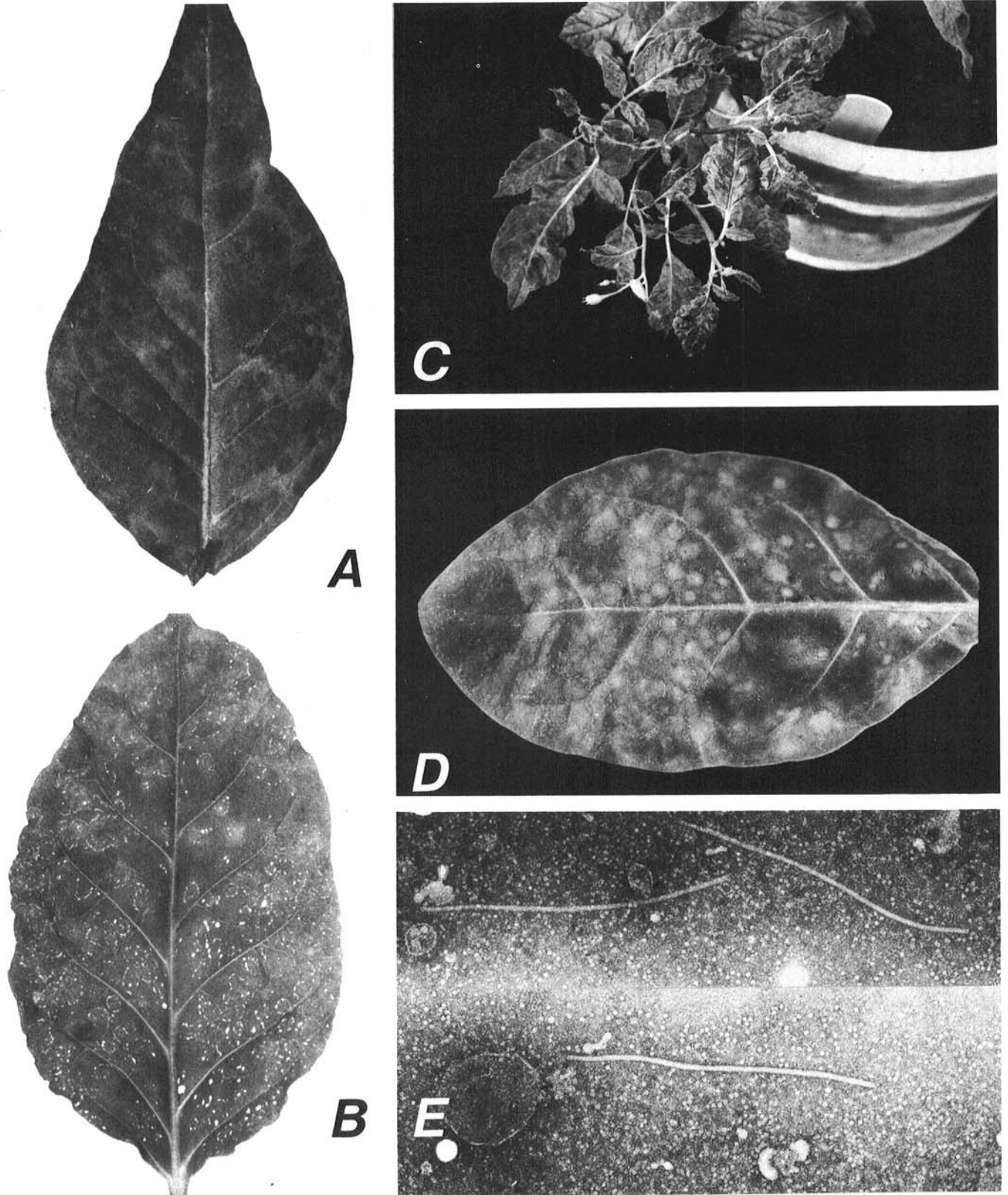


Fig. 1. Symptomatology and electron microscopy of wild potato mosaic virus. **A)** Mosaic symptom in *Nicotiana clelandii*. **B)** Systemic necrotic spotting, rings and line patterns in tobacco cultivar Samsun. **C)** Naturally infected plant of *Solanum chancayense* collected from the lomas vegetation showing leaf deformation and strong mosaic. **D)** Local chlorotic blotches and brown necrotic rings in *Nicotiana rustica*. **E)** Electron micrograph of particles in diluted infective sap of *Nicotiana occidentalis* $\times 60,000$.

TABLE 3. Homologous and heterologous serological reactions between wild potato mosaic virus and several other viruses of the potato virus Y group

Antiserum	Antigen									
	WPMV	PTV	PVY	PVA	TVMV	TEV	PVMV	CDV	HMV	
WPMV	1,024 ^a	64	64	256	16	64	32	8	4	
PTV	8	64								
PVY	8		64							
PVA	0			1,024						
TVMV	32				256					
TEV	0					1,024				
PVMV	0						1,024			

^aReciprocal values of titers in microprecipitin grid tests.

thin white necrotic rings. *Nicotiana rustica* therefore seems a useful host for distinguishing WPMV from other potyviruses.

Aphid transmission. WPMV was readily transmitted by *M. persicae* from infected to healthy *N. bigelovii* using acquisition periods of 30 sec or 1 min. For example, in a test in which 20 aphids were given 30 sec acquisition feedings on an infected *N. bigelovii* source plant, placed singly onto individual *N. bigelovii* plants and left for 1 hr before kill with insecticide, 14/20 plants became infected. In further tests using 30 sec acquisition periods, aphids readily transmitted WPMV from infected *N. bigelovii* to *N. bigelovii* and to *S. mochicense* but not to plants of *N. glutinosa*, *Physalis peruviana*, or potato cultivars Chata Blanca and Merpata. Similarly, the virus was transmitted readily from infected to healthy *S. chancayense* but not to potato cultivar Mariva.

Attempted graft transmission to *Solanum tuberosum*. Because WPMV failed to infect *S. tuberosum* cultivars by either mechanical or aphid inoculation, infected scions of *S. chancayense* were grafted onto plants of cultivars Arran Pilot and Chata Blanca. No graft transmission of the virus to these cultivars occurred.

Properties in sap. Infectivity in *N. clevelandii* sap was lost by diluting to 10^{-4} but not to 10^{-3} in distilled water, by heating for 10 min at 65 C but not at 60 C, and by storage at about 20 C for 6 days but not for 5 days. When *N. clevelandii* leaves were desiccated and held over silica gel or stored frozen at -20 C, infectivity was maintained for at least 6 mo and 1 yr, respectively.

Electron microscopy. Expressed sap from infected plants contained long flexuous particles (Fig. 1E). When 25 individual particles from infective *N. occidentalis* sap were measured, they ranged from 685 to 800 nm in length with a mean of 735 nm.

Serology. Wild potato mosaic virus antiserum had a titer of 1/1,024 in microprecipitin grid titrations using partially purified antigen and did not react against centrifuged healthy sap of *N. clevelandii*, *N. occidentalis*, or *N. debneyi*. It reacted with partially purified antigens of eight different potyviruses (Table 3) indicating that it is related to all of them. However, reciprocal tests showed that this relationship is only one-sided with PVA, PVMV, and TEV. Taking into consideration both the homologous and heterologous titers the results suggest that WPMV is more closely related to PTV, TVMV, and PVY than to any of the others.

DISCUSSION

Wild potato mosaic virus resembles other members of the potyvirus group in particle size and shape, in its properties in infective sap and in being readily acquired in brief probes by aphids (4). Moreover, it is serologically related to eight other potyviruses from solanaceous hosts, showing closest affinities to PTV, PVY, and TVMV. Wild potato mosaic differs from PTV and PVY, however, in having an unusually narrow host range restricted to certain species in five genera of the Solanaceae (*Lycopersicon*, *Nicandra*, *Nicotiana*, *Physalis*, and *Solanum*). PTV and PVY infect species of Chenopodiaceae plus a wider range of Solanaceae, and PVY infects some leguminous species. Also, WPMV did not infect *L. pimpinellifolium* and clone A6 which are the most commonly used diagnostic hosts for PTV and PVY respectively

(3,5,7,8). TVMV, which also has a narrow range, differs from WPMV in failing to infect *N. clevelandii* and in causing different symptoms in all hosts which the two viruses have been shown to infect (tobacco, tomato, *N. debneyi*, *N. occidentalis*, and *P. floridana*) (5,9). Therefore WPMV seems to be sufficiently distinct to be considered for the present as a "new" potyvirus. However, future comparisons with other related potyviruses may lead to taxonomic regrouping of WPMV, PTV, and TVMV as distantly related strains of a previously named virus within the group (9).

Wild potato mosaic appears to be the first virus that has been studied from wild potatoes and differs from all other known potato viruses in not infecting the cultivated potato *S. tuberosum* even when inoculated by grafting. It seems well adapted to persist in the lomas of the Peruvian coastal desert, surviving from one winter to the next in dormant *S. chancayense* tubers underground. When the short-lived vegetation is present, the virus may be spread readily from one group of *S. chancayense* plants to another by *M. persicae* which often occurs in these areas. Its very narrow host range may have resulted from a long period of evolutionary adaptation for its isolated specialized habitat where only a limited number of plant species occur. Possible alternate hosts in the lomas include some *Nicotiana* and other *Solanum* species (10) and these may be reservoirs of the virus.

Wild potato mosaic virus caused a disease, similar to that in *S. chancayense*, in experimentally infected plants of *S. mochicense* which grows in the lomas of the northern coastal region (2). The virus possibly has a wider distribution than in *S. chancayense*, which is restricted to the lomas of the central coastal area, but surveys for it elsewhere have not yet been made.

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